Diversity and Ecology of Tropical Ectomycorrhizal Fungi in Africa 2

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Introduction

Contrary to general opinion some 20 years ago, ectomycorrhizal symbiosis is now considered to be very important in African ecosystems (e.g. Högberg and Piearce, 1986; Connel and Lowman, 1989; Buyck, 1994b). Ectomycorrhizas were demonstrated for the first time on roots of *Gilbertiodendron dewevrei* (De Wild.) Léonard, an important canopy tree in the Guineo-Congolian rainforest (Peyronel and Fassi, 1957). Later, ectomycorrhizas were also discovered on several other tree species and genera, including many characteristic miombo wood trees with *Brachystegia* spp. as the main component (Högberg and Nylund, 1981; Högberg, 1982; Högberg and Piearce, 1986; Thoen, 1993). Since then the study of ectomycorrhizas in tropical Africa has gained much interest but has mostly concentrated on the host trees. A review of the history of ectomycorrhizal research in tropical Africa is given by Fassi and Moser (1991).

Although the taxonomic knowledge of these fungi is very incomplete and their ecology has not yet been studied, some preliminary observations on the taxonomic diversity, ectomycorrhizal status, host specificity, geographic distribution, ecological range and phenology can be made.

The observations presented here were mainly based on a detailed revision of tropical African *Lactarius* by the first author, which involved about 1000 collections from 130 sites in 18 countries. An important part of the collecting was undertaken by the second author in miombo woodlands in northern Zambia and Burundi (Rumonge district). Extrapolations to other genera and quantitative estimations were based principally on unpublished field observations and existing collections of still undescribed species and, to a lesser degree, on literature data.

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Taxonomic Diversity of the Ectomycorrhizal Fungi

The ectomycorrhizal fungi in tropical Africa are represented principally by *Amanita* Pers., *Cantharellaceae*, *Russulaceae* and *Boletales*, and to a lesser degree by hypogeous fungi, gasteromycetes, *Cortinariaceae* and *Gomphales* (Thoen and Bâ, 1989; Thoen and Ducousso, 1989; Buyck *et al.*, 1996; personal observations). Taxonomic knowledge of these groups is incomplete but advancing.

The genus *Lactarius* presently contains 83 accepted species and two varieties in tropical Africa (Karhula *et al.*, 1998; Verbeken, 1995, 1996a,b,c,d, 1998a,b, 2000; Verbeken *et al.*, 2000; Verbeken and Walleyn, 2000), but it is estimated that the total number of *Lactarius* in the African tropics exceeds 150 species. The number of undescribed collections in examined herbaria suggests at least 60 *Lactarius* species for the Zambezian and Sudanian woodlands alone. A similar number of *Lactarius* species is likely to be found in African, dense forest types. Taking into account that, even for a well-explored continent such as Europe, 21 new *Lactarius* species have been described since 1980, the above estimate can still be considered to be very conservative.

Table 2.1 compares the *Russula–Lactarius* species ratio (R/L) from a number of areas both in and outside Africa. Although the areas considered are very different in scale and exploration rates, the ratio (between 2.0 and 2.5) seems to be fairly constant and independent of continent or vegetation type. The total number of *Russula* species in tropical Africa (see Table 2.2) is estimated to range between 285 and 350 species so, taking into account the estimated number of *Lactarius* species, at least 400–500 species of *Russulaceae* are involved in ecto-

Table 2.1. A comparison between described *Russula* (R) and *Lactarius* (L) species in various parts of the world.

Area studied	No. of R	No. of L	R:L	Source
Europe	± 350	± 150	± 2.3	Courtecuisse and Duhem (1994)
Tropical Africa	165	85	1.9	Table 2.2
Germany	154	81	1.9	Krieglsteiner (1991)
Netherlands	118–128	56	2.1–2.3	Arnolds *et al.* (1995)
African rainforests	110	41	2.7	Buyck (1993,1994a, 1997); Verbeken (1996d)
South-east England	107	60	1.8	Dennis (1995)
Melle (Belgium), Geerbos	37	15	2.5	R. Walleyn (Gent, 1999, personal communication)
Australia	37	15	2.5	May and Wood (1997)
Madagascar	27	12	2.3	Heim (1938)
Shetland Isles[a]	9–10	3	3–3.3	Watling (1992)
Burundi, Rumonge	69%	31%	2.2	Buyck and Verbeken (1994)

[a]Introduced species excluded.

mycorrhizal symbioses in the vast forest and woodland areas throughout tropical Africa. The number of *Russulaceae* from tropical Africa, then, more or less equals that described from Europe.

Table 2.2 compares the number of described taxa accepted and the estimated total number of taxa for the other groups of ectomycorrhizal fungi in tropical Africa. From these data it seems that at least 400 ectomycorrhizal species remain to be described. This relatively low number can be explained by the paucity of ectomycorrhizal *Cortinariaceae* and *Tricholomataceae* in Africa; both families account for several thousands of species in the Northern Hemisphere.

Endemism of Tropical Ectomycorrhizal Fungi in Africa

None of the *Lactarius* and *Russula* species from indigenous, African forests and woodlands has been found elsewhere in the world. Earlier reports of European

Table 2.2. Main putative ectomycorrhizal fungi (EM) of tropical Africa.

	No. of taxa identified	Estimated no. taxa	Main references
Cantharellaceae	35–40	> 60	Heinemann (1958, 1966a); Eyssartier and Buyck (1999a,b)
Lactarius	85	> 125	Heim (1938, 1955); Verbeken (1995, 1996a,b,c,d, 1998a,b); Verbeken and Walleyn (2000); Verbeken *et al.* (2000); Karhula *et al.* (1998)
Russula	± 165	> 285	Heim (1938); Buyck (1993, 1994a, 1997, 1999); Härkönen *et al.* (1993)
Boletales[a]	140–145	> 200	Heinemann (1954, 1966b); Heinemann and Rammeloo (1980, 1983, 1986, 1987, 1989a,b); Watling and Turnbull (1993, 1994)
Amanita[a]	50–55	> 70	Beeli (1935); Härkönen *et al.* (1994); Pegler and Shah-Smith (1997); Walleyn and Verbeken (1999)
Cortinarius	1	> 10	Beeli (1928)
Inocybe	8	> 25	Pegler and Rayner (1969); Buyck and Eyssartier (1999)
Scleroderma	8	± 10	Dissing and Lange (1962); Demoulin and Dring (1971, 1975)
Sequestrate fungi	11	> 15	Castellano *et al.* (2000)
Total	± 410[b]	> 800	

[a]Probably including some non-mycorrhizal species.
[b]Excluding miscellaneous putative EM fungi (e.g. *Terfezia*, *Thelephoraceae* and *Coltricia*).

species were found to be misidentifications. We can, therefore, conclude that, to the best of our knowledge, the *Lactarius* and *Russula* mycota of tropical Africa is unique and completely endemic. This mycota is apparently also incompatible with exotic tree plantations, as only introduced fungi fruit in association with these foreign hosts; for example, *Russula pectinatoides* Peck (a temperate species) in Tanzanian pine plantations (Maghembe and Redhead, 1980; Härkönen *et al.*, 1993). An equally high degree of endemism is observed in most other groups of African ectomycorrhizal fungi (e.g. Robyns, 1935–1972; Heinemann and Rammeloo, 1972–1997; Buyck and Eyssartier, 1999) with the exception of *Scleroderma*, most reported species of which have a pantropical or almost cosmopolitan distribution. Interestingly, the few species reported from both tropical Africa and another continent, such as *Amanita hemibapha* (Berk. & Br.) Sacc., *Craterellus aureus* Berk. & M.A. Curtis or *Rubinoboletus balloui* (Peck) Heinem. & Rammeloo, belong to taxonomically critical complexes.

Some species have been recorded from both Madagascar and the African continent (e.g. *Lactarius rubroviolascens* R. Heim, *Russula gossypina* Buyck), but from the data available it is difficult to compare the ectomycorrhizal mycobiota of both areas, which have no host tree species in common.

On the other hand, close systematic affinities with species from other continents are obvious at the infrageneric level. In the case of *Lactarius*, examples are sections *Lactariopsidei* (tropical America), *Chamaeleontini* (South-east Asia), *Plinthogali* (Europe, North America, Asia) and *Rugati* (North Africa, Europe, Asia, North America, tropical America). The occurrence of the conspicuous secondary angiocarpic *Lactarius* species (section *Lactariopsidei*) in both tropical Africa and America is one of several resemblances observed between the mycobiota of these two regions (e.g. Guzmán *et al.*, 1989), suggesting an earlier link between the distributions of some fungi and some angiosperm genera (Watling, 1993).

The early isolated position of the African continent has undoubtedly resulted in several centres of diversification of tropical ectomycorrhizal fungi. The deserts in the north are a natural barrier for the migration of most ectomycorrhizal fungi and apparently no, or very few, indigenous ectomycorrhizal host plants occur in southern Africa (e.g. see Allsopp and Stock, 1993). All South African *Lactarius* and *Russula* species are associated with introduced *Pinus* (Doidge, 1950; Pearson, 1950; van der Westhuizen and Eicker, 1987, 1994) and are likely to be introduced along with their host (including *Russula capensis* A. Pearson, which is considered, most probably, to be identical to a European or North American species).

Nevertheless, indigenous ectomycorrhizal fungi might be present in southern Africa as some members of traditionally presumed ectomycorrhizal genera (*Amanita*, *Phlebopus*) occur in natural vegetation types in South Africa (Baxter, 1990; Reid and Eicker, 1991; van der Westhuizen and Eicker, 1994). The nutritional mode of such fungi needs investigation: a mycorrhizal relationship with

herbaceous plants cannot be excluded, as has been shown for *Terfezia pfeilii* Henn. in Botswana (Taylor *et al.*, 1995). Furthermore, *Amanita foetidissima* D.A. Reid & Eicker, reported from Zambia (Pegler and Shah-Smith, 1997), is described as forming fairy rings in grasslands, away from any potential host tree (Reid and Eicker, 1991), and several *Phlebopus* typically sporulate in cultivated land or garden lawns.

Do All Tropical African Putative Ectomycorrhizal Species form Ectomycorrhizas?

Several species in these genera have sometimes been collected on rotten wood in various stages of decay. Basidiomes of *Lactarius gymnocarpus* R. Heim ex Singer were observed even 1 m up large tree stems in Korup National Park, Cameroon (R. Watling, Edinburgh, UK, 1994, personal communication). Sometimes these fungi with a 'lignicolous' habit are considered to be (facultative) saprotrophs (Singer, 1986). However, both Thoen and Watling independently observed mycelial links of 'lignicolous' *L. gymnocarpus* basidiomes with tree rootlets (R. Watling, Edinburgh, UK, 1994, personal communication; D. Thoen, Brussels, Belgium, 1998, personal communication). This 'lignicolous' habit is not restricted to the African tropics and has also been observed in tropical America (e.g. *Lactarius neotropicus* Singer: Pegler and Fiard, 1979), North America (e.g. *Lactarius vietus* (Fr.: Fr.) Fr., *Lactarius louisii* Homola : Hesler and Smith, 1979), Europe (e.g. *Lactarius camphoratus* (Bull.: Fr.) Fr.: Bresinsky and Stangl, 1970) and Asia (e.g. *Lactarius lignicola* W.F. Chiu: Chiu, 1945). Unpublished observations of the authors indicate a similar phenomenon in *L. vietus*, *L. camphoratus*, *Lactarius tabidus* Fr. and *Lactarius glyciosmus* (Fr.: Fr.) Fr.. As Hesler and Smith (1979) stated, 'it is common knowledge that the rootlets of trees often penetrate wet rotten logs and there show a profuse formation of mycorrhiza. The adaptation is one favouring both adequate moisture and air for the life processes of both host and fungus, and the basidiocarps near this centre of activity'. The 'lignicolous' habit is generally observed where the fitness of the ectomycorrhizal nutritional mode becomes more critical such as in very wet and poor soils (e.g. in swamp borders and riparian forest), burnt soils and rainforests (where the competition for nutrients is higher). This niche above ground level is also suggested as an adaptation to seasonally waterlogged sites (Singer and Araujo, 1986). African *Lactarius* species fruiting on wood have only been observed in dense forest, and not in other woodland types; indeed the 'lignicolous' habit is not a constant characteristic of most species studied in this respect. In African *Lactariopsis* and South American and Asian *Pleurogala* this character was over-emphasized as a character to distinguish between genera (Buyck and Horak, 1999).

Therefore, it is concluded that all African *Lactarius* species found so far form ectomycorrhizas. A similar conclusion is accepted for *Russula* and most other genera with known ectomycorrhizal members.

Distribution Patterns of *Lactarius* Species in Africa

In North America (Hesler and Smith, 1979) and Africa (this study), a possible preference of certain *Lactarius* species for certain soil types (e.g. acid or calcareous), a character frequently stressed in Europe (e.g. Verbeken *et al.*, 1999), has received less attention.

Phytogeographic regions are also important for the distribution patterns of fungi. In Europe, several *Lactarius* species are restricted to the Mediterranean area (e.g. *Lactarius cistophilus* Bon & Trimbach), the arctic–alpine zone (e.g. *Lactarius dryadophilus* Kühner), the boreal zone (e.g. *Lactarius hysginoides* Korhonen & T. Ulvinen) or to the atlantic–temperate zone (e.g. *Lactarius circellatus* Fr.). Similarly, Hesler and Smith (1979) distinguished four 'mushroom provinces' in North America in which a large number of endemics have evolved. The author's observations for tropical Africa suggest a high phytogeographical and ecological specificity. Although many regions of tropical Africa remain mycologically unexplored (e.g. Sudanian woodlands), it is evident that most *Lactarius* species, also *Russula* (Buyck, 1999) and most other ectomycorrhizal groups, have been collected either in open (miombo, *Uapaca* woodland) or in dense forest types (e.g. rain-, riparian, gallery, swamp and dry evergreen forests) but rarely in both (Table 2.3).

A relatively large number of species (e.g. *Lactarius brunnescens* Verbeken, *Lactarius densifolius* Verbeken & Karhula, *Lactarius edulis* Verbeken & Buyck, *Lactarius heimii*, *Lactarius longisporus* Verbeken, *Lactarius medusae* Verbeken, *Lactarius urens* Verbeken, *Lactarius velutissimus* Verbeken & Buyck) seems to be restricted to the Zambezian region as defined by White (1983). The Sudanian region, although poor in ectotrophs and lacking important mycorrhizal tree genera such as *Brachystegia* and *Julbernardia* (Thoen, 1993), remains to be explored, but the recent discovery in Benin of *Lactarius kabansus* Pegler & Piearce and *Lactarius gymnocarpoides* Verbeken, both common species in the Zambezian area, suggests the existence of a number of species that occur in both Sudanian and Zambezian woodland.

Again the distribution of *L. gymnocarpus* suggests that the Guineo–Congolian region is another centre of endemic mycorrhizal fungi (Fig. 2.1), which could be extended to the East Malagasy region as demonstrated by *Lactarius acutus* R. Heim, *Lactarius melanogalus* R. Heim ex R. Heim, *Lactarius rubroviolascens* R. Heim and *Lactarius annulatoangustifolius* (Beeli) Buyck. Specialized vegetation such as *Uapaca* gallery forest possibly allows Guineo-Congolian ectomycorrhizal fungi to invade the Zambezian region. Apparently,

Table 2.3. Phytogeographical and ecologial specificity of African *Lactarius* species: occurrence of the known species in woodland ecosystems (WL: miombo woodland, Sudanian woodland) and forest ecosystems (RF: rain-, dry evergreen, gallery and swamp forests). +: all collections studied, (+): minority of collections studied.

	WL	RF		WL	RF
acutus		+	*longipes*		+
adhaerens		+	*longisporus*	+	
albocinctus	+		*luteopus*	+	
amarus		+	*medusae*	+	
angustus		+	*melanodermus*		+
annulatoangustifolius	(+)	+	*melanogalus*		+
arsenei		+	*nonpiscis*	+	
atroolivinus	+		*nudus*		+
aurantiifolius	+		*orientalis*	+	
aureifolius	+		*pelliculatus*		+
badius		+	*phlebonemus*	(+)	+
baliophaeus	+	(+)	*phlebophyllus*		+
barbatus	+		*pisciodorus*		+
brachystegiae	+		*pruinatus*	+	
brunnescens	+		*pseudogymnocarpus*		+
caperatus		+	*pseudolignyotus*		+
carmineus	+		*pseudotorminosus*		+
chamaeleontinus	(+)	+	*pseudovolemus*		+
chromospermus	+		*pulchrispermus*	+	
claricolor		+	*pumilus*	+	
congolensis		+	*pusillisporus*	+	
corbula		+	*roseolus*	+	
cyanovirescens	+		*rubiginosus*	+	
denigricans	+		*rubroviolascens*		+
densifolius	+		*rumongensis*	+	(+)
edulis	+		*russuliformis*		+
emergens	+		*ruvubuensis*		+
flammans	+		*saponaceus*	+	
fulgens		+	*sesemotani*	+	(+)
var. *africanus*		+	*striatus*		+
goossensiae		+	*subamarus*	+	
griseogalus	+		*sulcatulus*	+	(+)
gymnocarpoides	+		*sulcatus*	+	
gymnocarpus		+	*tanzanicus*	+	
heimii	+		*tenellus*	+	
hispidulus		+	*undulatus*		+
indusiatus	+		var. *rasilis*		+
inversus		+	*urens*	+	
kabansus	+		*velutissimus*	+	
kalospermus		+	*volemoides*	+	
kivuensis		+	*xerampelinus*	+	
laevigatus	+		*zenkeri*		+
latifolius		+			

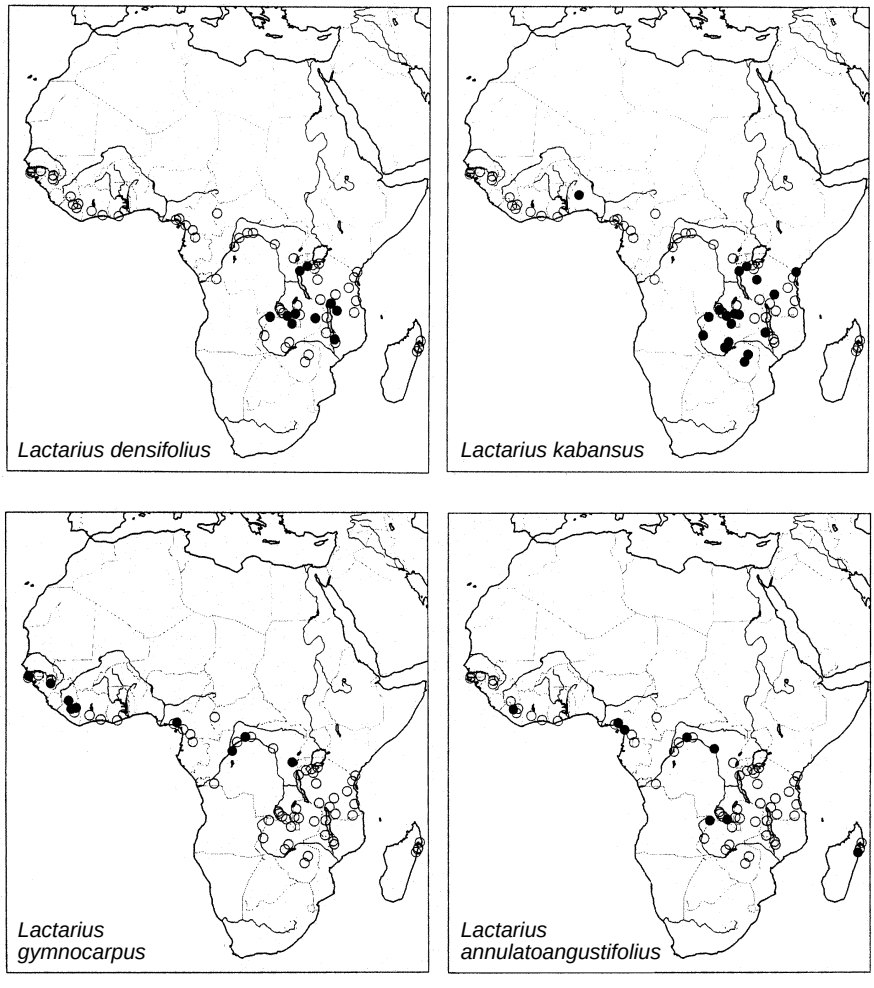

Fig. 2.1. Distribution of *Lactarius densifolius*, *L. kabansus*, *L. gymnocarpus* and *L. annulatoangustifolius*; open circle, collection sites; closed circle, taxon present.

the distribution of many African ectomycorrhizal fungi (including Madagascar) is linked to the contrast between open woodlands and dense forest.

Host Specificity

In Europe, with its numerous monospecific or species-poor forests, many *Lactarius* species are associated with only one tree genus (e.g. *Lactarius salmonicolor* R. Heim & Leclair with *Abies*, *Lactarius quietus* (Fr.: Fr.) Fr. with *Quercus*, *Lactarius lilacinus* (Lasch: Fr.) Fr. with *Alnus*). Literature data, herbarium notes

and the author's own field observations suggest that this host specificity is lacking in Africa. Most *Lactarius* species fruit under several tree genera in African forests, which are usually much richer in tree species than temperate forests (Thoen and Bâ, 1989; Härkönen *et al.*, 1993; Munyanziza and Kuyper, 1995; Buyck *et al.*, 1996), and this more generalist relationship can be extrapolated to most ectomycorrhizal fungi. More observations on monospecific tropical vegetation types might demonstrate the existence of a higher degree of specificity for some species, such as *Lactarius chromospermus* Pegler which has been collected exclusively under *Brachystegia* species at many localities (Buyck and Verbeken, 1995; Verbeken, 1996d; Verbeken *et al.*, 2000).

Phenology

Intensive collecting in the Rumonge region in Burundi made it possible to make some preliminary observations on the fruiting periodicity of *Lactarius* species in miombo woodland. An initial short period of rainfall (end of November–January) is usually separated from a long period of rain from (15 February) March to April (–15 May) by a short dry season (January–February). From the available data over a period of 3 years, it became clear that the fructification of several species is virtually confined to one of these wet periods (Fig. 2.2). In particular, *Lactarius barbatus* Verbeken and *L. densifolius* were collected only during the first rains. *L. kabansus* and *Lactarius subamarus* Verbeken were especially abundant at the beginning of this season, but were sporadically collected during the whole rainy season. In contrast, some species (such as *L. edulis*, *Lactarius rumongensis* Verbeken and *Lactarius pusillisporus* Verbeken) were collected only during the long period of rainfall. This second period yielded a higher number of species, but for a complete inventory in seasonally dry African forest collecting should cover both rainfall periods over several years.

Conclusion

At present, about 400 taxa of putative ectomycorrhizal fungi belonging to *Russulaceae*, *Boletales*, *Cantharellaceae*, *Amanita*, *Cortinariaceae*, various sequestrate fungi (Castellano *et al.*, 2000) and *Scleroderma*, have been described or reported from tropical African forests and woodlands, but it is estimated that at least another 400 taxa remain to be described. The mycorrhizal status seems doubtful for only a restricted number of *Amanita* species and boletes.

Except for *Scleroderma*, a very high proportion of the species are endemic to the studied area (including Madagascar). Judging from an extensive taxonomic study of the genus *Lactarius* (*Russulaceae*), a high degree of host specificity, as known in temperate regions, appears to be absent, but many species are restricted to either woodland vegetation (miombo) or forest vegetation (rain-, dry evergreen and gallery forests). In miombo woodland, many species may

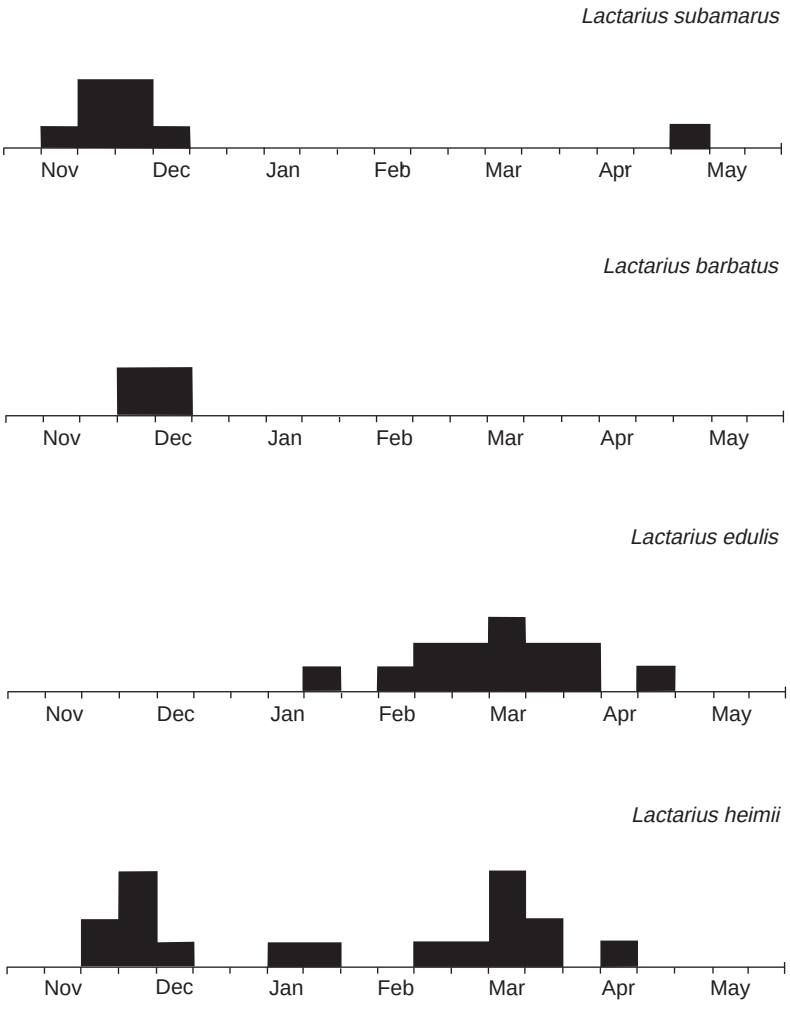

Fig. 2.2. Phenology (based on number of collections over a 3 year period) of *Lactarius subamarus*, *L. barbatus*, *L. edulis* and *L. heimii* in the Rumonge district (Burundi).

occur in a restricted area, but some species occur in both the Sudanian and the Zambezian woodland. Several miombo woodland species have a restricted fruiting period and occur during only part of the season.

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